

may be a nerve net and the large object could be part of a magnetic receptor.

In other dolphins no large particles were found which permitted the type of analysis described. These samples did not exhibit the multidomain magnetite transition on warming from liquid nitrogen temperature, but showed a gradual decrease of magnetization. This is consistent with the presence of fine superparamagnetic and near superparamagnetic single-domain magnetic material.

We conclude that certain dolphins have magnetic material in their dura mater. Some of this is magnetite and may be used as a magnetic field receptor. However, the material is so magnetically soft that it is unlikely to be analogous to a permanently magnetized compass needle. Still, a soft anisotropic magnetic material will experience a torque in the geomagnetic field because of its induced moment. This could serve as a basis for field detection. Alternatively, the seemingly fragile nature of the material suggests that it might deform in the earth's field. This, too, could be utilized for field reception (4). We do not know whether the magnetite is part of a field receptor system or whether dolphins can detect a magnetic field. Nevertheless, the association of apparent nerve fibers with the magnetite suggests that the magnetite is not simply a metabolic by-product but has a sensory function.

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Stromatoporoid Growth Rhythms and Rates

Abstract. *Stromatoporoids are major contributors to framework construction in Paleozoic reefs. The Devonian species *Parallelostroma densilaminata* (Fagerstrom), *P. winchelli* (Galloway and Ehlers), and *Stictostroma* sp. form large rhythmically structured colonies that competitively overgrow corals. Their competitive interactions and important role as reef builders place considerable value on growth rate information. Identification of common growth periods in these interacting species provides a method for quantifying vertical and lateral stromatoporoid growth and a means for identifying an annual periodicity of calcification.*

Organisms that secrete accretionary skeletons record rhythmic motions of an astrophysical or geophysical nature if there is differential growth over the duration of the rhythmic event. Deposition of new material in these organisms occurs along the skeletal margins exclusively (1, 2) and in direct response to regular environmental changes that accompany rhythmic phenomena (2, 3). Two rates of physical growth usually exist, each producing a characteristic structural density of hard parts (3-5). Consequently, all such organisms have skeletons imprinted with a structural periodicity matching that of some external rhythm. Although the ecological factors that influence the biomineralization processes remain unknown, the skeletal structural periodicity constitutes a long-term growth rate record that can be measured once the periodicity of the rhythm is identified.

Parallelostroma densilaminata (Fagerstrom), *P. winchelli* (Galloway and Ehlers), and *Stictostroma* sp. are three encrusting stromatoporoids which, along with corals, are major frame builders in middle Devonian patch reefs of Michigan. All of the stromatoporoids are frequently found encrusting corals either as a postmortem or competitive overgrowth (6). Each of the mantling stromatoporoids has a massive skeleton (coenosteum) with internal structures of two distinct but unknown frequencies. The

fundamental cyclic structure (laminae), which is not always clearly distinguishable, consists of a thin sheet of calcareous skeletal elements. A longer duration rhythmic structure (latilaminae) is defined by bands of closely spaced laminae. These make up concentric sheets with a maximum thickness of 1 to 7 mm. Succeeding latilaminae are characteristically distinguished by a variation in color and an accompanying increase in laminae density. This kind of physical change in growth suggests that stromatoporoid skeletogenesis was rhythmic in nature and responsive to some external rhythm with a matching periodicity. There is also an indication that skeletal calcification was rapid. The competitive overgrowth of one organism by another must involve differential growth along interspecific skeletal margins (7). Thus, there is the implication that stromatoporoids grew faster than the corals they mantled.

Both hypotheses can be evaluated by the use of competitively intergrown specimens to define common periods of growth. Fossils recording this type of interaction bring the known periodicities of coral skeletons (coralla) (4, 5, 8) into juxtaposition with the unknown periodicities of rhythmically organized, mantling, stromatoporoid coenosteia. Growth periods common to both animals are readily defined by two or more successive steplike interfaces that involve bas-

Table 1. Stromatoporoid growth rates.

Stromatoporoid and coral species	Total number of individual specimens	Coral growth (mm/year)	L_s/V_c	V_s/V_c	Stromatoporoid growth	
					Lateral (mm/year)	Vertical (mm/year)
<i>P. densilaminata</i> on <i>F. alpenensis alpenensis</i>	5	10.6	2.18	0.23	23.1	2.5
<i>P. densilaminata</i> on <i>Thamnopora</i> sp. A	1	7.9	1.67	0.33	13.2	2.2
<i>P. densilaminata</i>	13					2.5*
<i>P. winchelli</i> on <i>F. alpenensis alpenensis</i>	1	11	1.43	0.27	15.7	3.0
<i>P. winchelli</i>	35					3.8*
<i>Stictostroma</i> sp. on <i>Thamnopora</i> sp. A	5	7.9	1.32	0.16	10.4	1.3

*Latilaminae measurements

al laminae in the stromatoporoid (Fig. 1A). Each of these points marks the beginning and end of growth in the stromatoporoid and coral, respectively. Three measurements are made for each growth increment: (i) vertical linear growth in the stromatoporoid (V_s), (ii) vertical linear growth in the coral (V_c), and (iii) lateral linear growth in the stromatoporoid (L_s) (see Fig. 1A). For a selected interval, V_s is equal to the distance between the two basal laminae and L_s corresponds to the arcuate distance between two actual coincident or extrapolated growth bands. The relative vertical and lateral growth in stromatoporoids can then be compared with the vertical growth rate of the mantled coral and expressed as the ratios V_s/V_c and L_s/V_c , respectively. Absolute stromatoporoid growth can then be calculated by multiplying these values by the average annual growth rate of the coral. An annual rate of growth for fossil corals is determined by measuring the skeletal segment between periodic decreases in dissepiment size (4) or tabular spacing (5) and arcuate growth bands exhibited by many tabulate corals.

Results of these measurements (Table 1) show a consistent trend of slow vertical but very rapid lateral stromatoporoid growth. *Parallelostroma densilaminata* has the fastest lateral growth and the most extreme range in the rates of calcification between the two directions of growth, differing by a factor of 10. A similar variation exists in the rate of skeletogenesis of *Stictostroma* sp., but this species records the smallest vertical growth rate of the three species. The largest vertical growth rate (3 mm per year), based on laminae, characterizes *P. winchelli*, which contributes to its having the lowest L_s/V_s ratio.

Two kinds of additional data support the absolute growth rate values and the variation in the rates of calcification that were calculated. First, there is good agreement in the absolute vertical growth rates of *P. densilaminata* calculated from specimens which used different coral species as a substrate even though each coral had its own growth rate. The fact that there is a marked difference between the calculated lateral rates of stromatoporoid growth as determined by the different corals (Table 1) does not discredit the results. In fact, this difference adds credence to the data since differences in the rate of lateral but not vertical growth might be expected for a *Parallelostroma* that is competing for living space against different coral species. An excellent analogy exists in

the hierarchical arrangement of inter-specific digestive dominance in living scleractinian corals (9). A slow vertical growth rate and correspondingly rapid lateral growth rate is also clearly evidenced by the stromatoporoid overgrowth pattern (Fig. 1B) of an entire *Favosites* corallum more than 3 cm in diameter that was encrusted by a *P. densilaminata* without a significant vertical development of the coenosteum.

The hypothesis that latilaminae have a matching external periodicity—such as the annual periodicity suggested by Galloway (10)—was confirmed when calculated annual vertical growth rate values corresponded closely with the thicknesses of successive latilaminae (Table 1). The differences in the growth values (Table 1) are attributable in part to small sample size as well as genetic and ecological factors. Thus, it appears that the formation of latilaminae represents an annual event in stromatoporoids.

Stromatoporoids played important

roles in the growth and ecology of many mid-Paleozoic reefs and occupied the reef-building niche now filled by scleractinian corals. Elucidating the duration of latilaminae rhythms and growth rate characteristics of these extinct sponges (11) provides an important tool for further studies. Aside from its obvious use in further analysis of stromatoporoid growth, it should be possible to estimate growth rates and absolute times of duration for entire mid-Paleozoic reefs or reef complexes. Finally, this study may provide a framework for other investigations of geophysical rhythms in Paleozoic seas.

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6. F. O. Meyer, *Geol. Soc. Am. Abstr.* 10, 278 (1978); Presence-absence criteria identify the timing of stromatoporoid encrustations. Corals presumed dead prior to being overgrown by stromatoporoids generally show expected signs of corallite wear and breakage at the polypary surface. Sand and mud commonly infill corallites and coralla irregularities and thereby introduce a sediment film between the coral and stromatoporoid skeletons. Barring unusual conditions, where only part of the coral dies, most coralla have an even surface produced by skeletal growth during a single year. Stromatoporoids mantling nonliving corals have but one continuous lamina in contact with the substrate. Corals established on and eventually completely enclosed within the stromatoporoid provide a strong case for the simultaneous existence of both animals. Features of the contact zone from such specimens differ from those found in post-mortem overgrowths. Sediment and corallite damage are invariably absent from the overgrowth interface. Coralla surfaces are characteristically steplike and are the product of interference growth spanning several years. An inverse steplike basal surface is present in the nature of skeletal extension of the stromatoporoid. It has an onlapping geometry and several laminae contact the coral skeleton. Collectively, the criteria associated with competitive stromatoporoid encrustations of coral argue for the existence of protective coral polyp tissue at least until shortly before overgrowth occurred.
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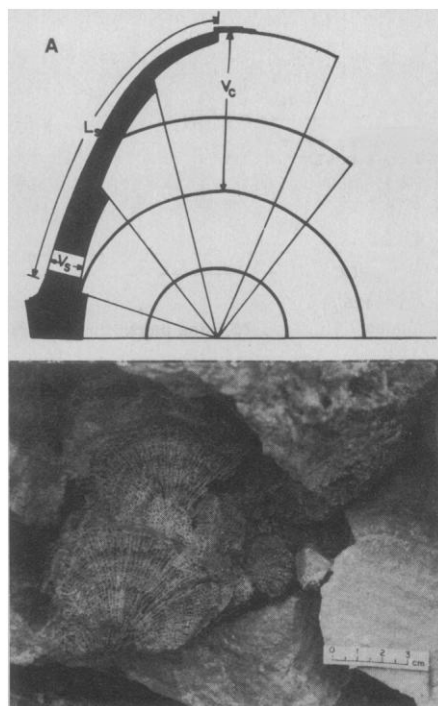


Fig. 1. Stromatoporoid-coral relationship. (A) Growth rate measurements on stromatoporoid-coral interactions. Arrows show positions of measurements and define common growth increments for each species. Arcuate lines represent annual growth bands. Measured are 2 years of vertical coral growth (V_c) and corresponding vertical (V_s) and lateral (L_s) stromatoporoid growth. (B) Stromatoporoid growth characteristics. A thin but laterally continuous sheet of stromatoporoid tissue separates the two *Favosites alpenensis* coralla. Both tabulate corals are completely enclosed within the stromatoporoid coenosteum. Growth banding within coral skeletons is evident.